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Embryonic and Larval Development of *Spisula solidissima similis* (Say, 1822) (Bivalvia: Mactridae)

by

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Abstract. Larvae of the southern surf clam, *Spisula solidissima similis* (Say, 1822), were reared in the laboratory at a salinity of 25 ppt and a temperature of 20–22°C through the embryonic and early larval development period. Unfertilized eggs averaged 58.5 ± 0.32 (SE) μm, with the size-frequency of eggs being normal. First polar body was observed 22 minutes after fertilization with 50% of eggs exhibiting polar bodies after 26 minutes. Ciliated blastula and trochophore stages occurred at 6 hours and 16.8 hours, respectively. Straight-hinge veligers appeared 39.2 hours after fertilization. Larvae grew to a mean size of 172 μm in the pediveliger phase (range 119 to 212 μm). Larvae were exhibiting active foot-probing by day 8 and continued to do so until day 13 when the cultures suffered heavy mortalities. Early life-history traits of *Spisula solidissima similis* larvae are compared to those for *Spisula solidissima solidissima* and *Spisula sachalinensis*.

INTRODUCTION

Unlike the commercially important Atlantic surf clam, *Spisula solidissima solidissima* (Dillwyn, 1817), the biology and ecology of the southern subspecies of the surf clam, *Spisula solidissima similis* (Say, 1822), has not been studied until recently. The southern surf clam has a maximum life span of 5 years (Walker & Heffernan, 1994) as compared to 37 years for the Atlantic surf clam (Sephton & Bryan, 1990), and attains a maximum size of 127 mm (Andrews, 1977) as compared to 226 mm in shell length for the Atlantic surf clam (Ropes & Ward, 1977). Southern surf clams mature sexually at age 1 year and at shell lengths of 40 mm (Kanti et al., 1993); whereas the Atlantic surf clam matures at 2 years of age and at a shell length of 67 mm (Belding, 1910). Southern surf clams from St. Catherines Sound, Georgia population spawned from February to May depending upon water temperature (Kanti et al., 1993). The Atlantic surf clam spawns in early summer to fall (Ropes, 1968; Jones, 1981). No early life-history data exists pertaining to larval development of this subspecies.

This study describes the embryonic and early larval development of *Spisula solidissima similis* reared within the laboratory. It compares the findings with the published life-history traits of *Spisula solidissima solidissima* (which is referred to in most shellfisheries literature as "*Spisula solidissima*") and *Spisula sachalinensis* (Schrenk, 1862).

MATERIALS AND METHODS

Southern surf clams, *Spisula solidissima similis,* were collected from a field population occurring in St. Catherines Sound, Georgia, on February 6, 7, and 8, 1994. Animals were dredged from a depth of approximately 8 m. Animals were planted in 12 mm mesh 1 × 1 × 0.25 vinyl-coated wire cages partially buried in a sandy-mud substrate on an intertidal flat located at the mouth of House Creek, Wassaw Sound, Georgia, on 9 February 1994. Cages with animals were positioned at the spring low-water mark. On 9 March 1994, clams were brought into the hatchery and placed in conditioning tanks (450 L) which were maintained at 25 ppt and 20–21°C. Animals were fed *Isochrysis galbana* (Tahitian isolate) on a daily basis.

On 7 April 1994, 10 animals were injected with 0.2 mL of serotonin in the anterior adductor muscle. After injection, each animal was placed in a separate container. Eight individuals (four males and four females) began spawning within 1 to 2 minutes after injection. The remaining two clams did not spawn. Samples of eggs from each spawned female were obtained, and 30 eggs per female measured

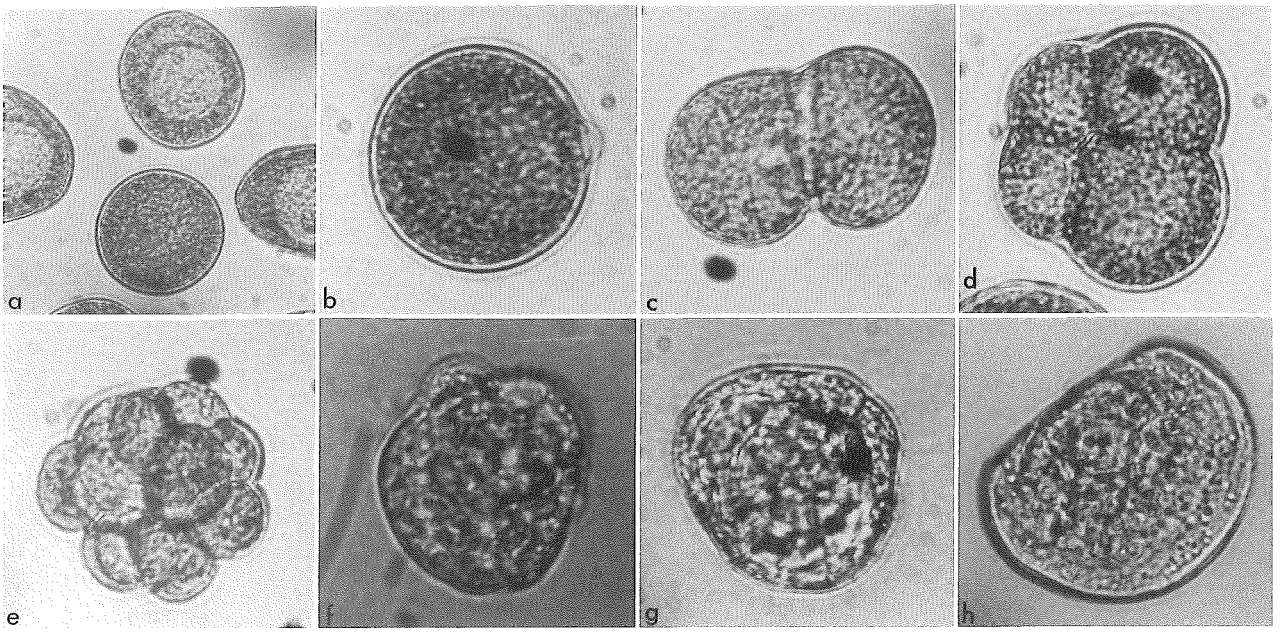

Figure 1

Photomicrograph of the various embryonic and larval stages of the southern surf clam, *Spisula solidissima similis* a) Unfertilized egg (approx. 58 mm); b) First polar body; c) First cleavage; d) Second cleavage; e) Multi-Cellular; f) Trochophore (approx. 78 mm); g) Gastrula; and h) Veliger (approx. 80 mm).

for size. Sperm and eggs were pooled into separate containers.

A 10 liter egg suspension was fertilized with sperm. Embryonic development was observed by placing a 1 mL subsample of eggs on a Zeiss Axiovert 10 microscope (at ×10 and ×32 and visually monitoring development. Various embryonic stages were compared to those described for *Spisula sachalinensis* by Imai et al. (1983). Fresh samples were observed every 15 minutes for the first two hours, with fresh samples observed every 30 minutes for the next 20 hours, after which the larvae were monitored on a daily basis. Once trochophore stages were reached, larvae were set up in three 10 L buckets at a density of 53 larvae per mL. Larvae were fed 100,000 cells per mL of *Isochrysis galbana* daily, and culture water exchanged every 48 hours. Every 24 hours, a 1 mL sample was visually checked to determine developmental stage, and 50 individuals were measured for shell length. Replicate ($n = 3$) 1 mL samples were taken, and the number of larvae per sample was enumerated every second day to give the mean stocking density per culture container.

RESULTS

A schedule of the main embryonic events is given in Table 1 with corresponding photomicrographs given in Figure 1. The mean diameter of the eggs prior to fertilization was 58.5 ± 0.32 (SE) μm. Germinal vesicle breakdown within the eggs was first observed 8 minutes after fertilization. The majority of the fertilized eggs had vesicle breakdown 10 minutes after fertilization. Hereafter, all of the times given are post-fertilization (t = 0 minutes), and the term "majority" refers to the fact that > 50% of the larvae displayed the described characteristic. First polar body formation occurred at 22 minutes with the majority of

Table 1

Embryonic development event times of *Spisula solidissima similis* cultured in 25 ppt and 20–22°C seawater.

Stage description	First occurrence time	> 50% occurrence time
Fertilization	0	0
Germinal vesicle breakdown	8 min	10 min
First polar body	22 min	26 min
First division	26 min	41 min
Second division	75 min	89 min
Third division	96 min	115 min
Ciliated blastula	5.5 hr	6 hr
Gastrula	8 hr	8.7 hr
Early trochophores	15.1 hr	15.1 hr
Trochophores	16.4 hr	16.8 hr
Veliger	28.5 hr	39.2 hr
Rudimentary foot		7 days
Probing foot		7.5 days

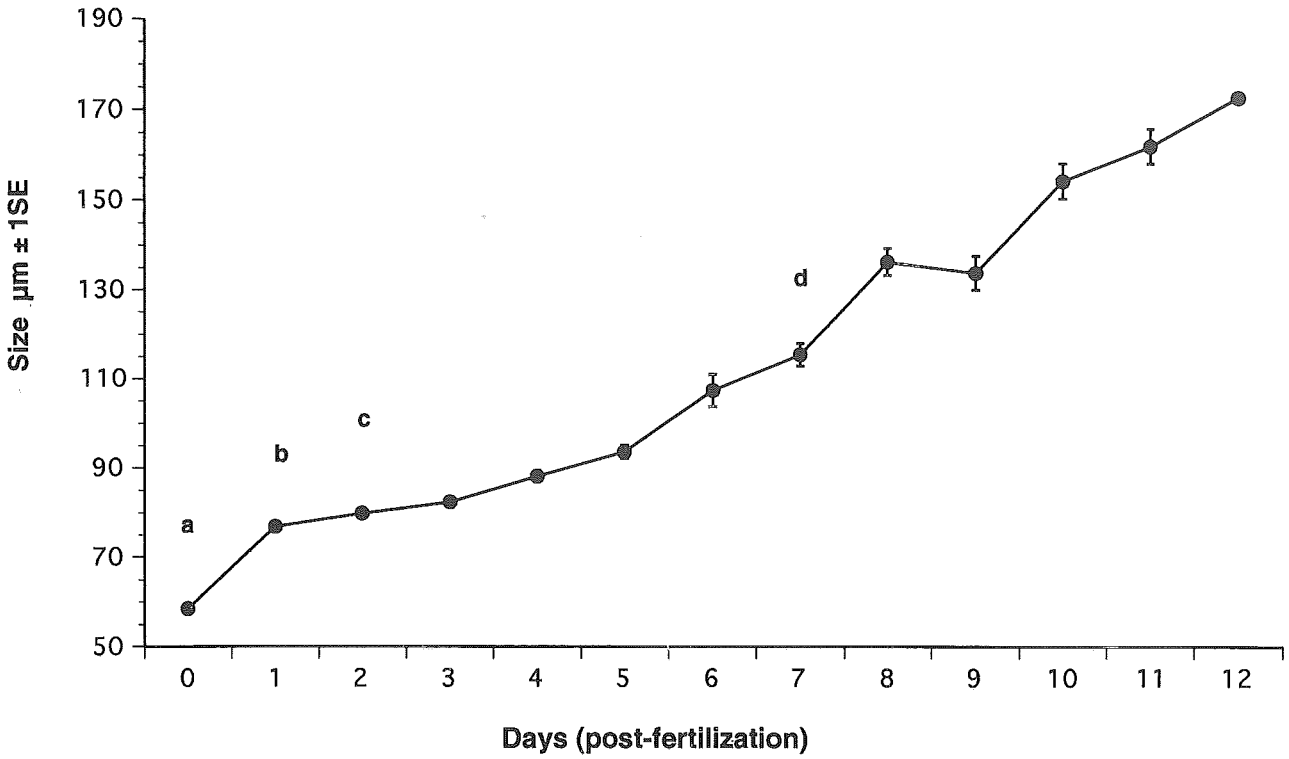

Figure 2

Growth of *Spisula solidissima similis* larvae and juveniles in µm ± one standard error (SE) from egg to day 12. a) Eggs; b) Trochophores; c) D-Shaped larvae; and d) Foot-Probing first exhibited.

individuals displaying polar body formation at 26 minutes. The majority of the larvae displayed first cleavage, second cleavage, and third cleavage at 41 minutes, 89 minutes, and 115 minutes, respectively. Free-swimming blastula larvae were observed at 6 hours, and first invagination of the archenteron occurred at 8 hours, with the majority displaying gastrula characteristics (multicellular, actively motile with rudimentary gut formation) at 8.7 hours. The first early trochophores were observed at 15.1 hours. The majority of the larvae were trochophores at 16.1 hours. At this stage, the larvae had a mean size of 76.8 ± 0.11 (SE) µm. Straight-hinged larvae were first observed at 28.5 hours with the majority D-shaped at 39.3 hours. A rudimentary foot was observed at 7 days, when the clams had a mean size of 107.3 ± 3.62 (SE) µm. A partially developed foot was observed probing (extending beyond the margin of the shell) at 7.5 days. The larvae continued as motile pediveligers until 12 days after fertilization. During this time, the larvae were primarily observed as swimmers. Some larvae exhibited foot-probing behavior on the surface of the slide, i.e., moving about with the aid of foot extension and velar activity. However, at 13 days, heavy mortality of the larvae was experienced due to contamination within the culture vessels by protozoans, probably brought in with food. The experiment was then terminated. Growth of the larvae through the 12 days of the study is recorded in Figure 2. Larval densities in the rearing containers ranged from mean values of 53, 47, 46, 33, and 26 larvae per mL on days 1, 3, 5, 7, and 9, respectively.

Table 2

Mean egg diameter in µm and egg size range of various species of *Spisula*.

Species	Mean egg diameter	Range in µm	Reference
Spisula sachalinensis		70–75	Imai et al., 1953
S. s. solidissima	56.5		Loosanoff & Davis, 1963
S. s. solidissima	53		Schechter, 1941
S. s. solidissima	56		Allen, 1853
S. s. solidissima		53–56	Costello et al., 1957
S. s. solidissima	58.3	50–69	Walker, unreported data
S. s. similis	58.5	44–78	This study
Spisula subtruncata		50–55	Jorgensen, 1946

Table 3

Embryonic and larval development event times of various *Spisula* species.

Stage description	*S. sachalinensis* Imai et al., 1983	*S. s. solidissima* Allen, 1953	*S. s. solidissima* Ropes, 1980	*S. s. solidissima* Schechter, 1941	*S. s. similis* This study
Fertilization	0	0	0	0	0
First polar body	40–50 min	29 min		30 min	26 min
First division	1.5 hr	74 min		65 min	41 min
Second division	2.5 hr	99 min	90 min	95 min	89 min
Third division	3.5 hr		110 min		115 min
Ciliated blastula		< 1 day		5 days	6 hr
Gastrula	12 hr		5.25 hr		8.7 hr
Trochophores	21 hr		9 hr		16.8 hr
Straight-hinge stage	40 hr		19–20 hr		39.2 hr
Pediveliger			18–21 days		> 8 days

DISCUSSION

The embryonic development of the southern surf clam, *Spisula solidissima similis,* is similar to that for *Spisula solidissima solidissima* and *Spisula sachalinensis.* The mean oocyte diameter for *S. s. similis* from this study was 58.5 ± 0.32 μm and did not differ significantly ($P = 0.5260$) in size from eggs spawned by *S. s. solidissima* ($\bar{x} = 58.3 \pm 0.13$ μm) cultured over winter in Georgia and induced to spawn via serotonin on the same day as *S. s. similis* in this study (Table 2). In addition, *S. s. similis* oocyte diameter was slightly larger than oocyte measurements reported for *S. s. solidissima* by Allen (1953), Loosanoff & Davis (1963), and Costello et al. (1957), but larger than that reported by Schechter (1941) (Table 2). *Spisula s. similis* oocyte diameters were larger than that reported for *S. subtruncata* (da Costa, 1778) (Jorgensen, 1946), but smaller than that for *S. sachalinensis* (Table 2).

Spisula solidissima similis embryonic development seems to occur at a comparable rate to that of *S. s. solidissima* through the third division, but seems to move at a slower rate for the gastrula through straight-hinge stages (Table 3). Yet it is unclear if the embryonic development times of Allen (1953), Schechter (1941), Ropes (1980), or Imai et al. (1983) are times at first occurrence or 50% occurrence. If they are first occurrence times, then *S. s. similis* embryonic development times from egg through third division proceeded at a slightly faster rate (Table 1) than that of *S. s. solidissima* (Table 3). *Spisula s. similis* appears to go through embryonic development up to the straight-hinge stage at a faster rate than *S. sachalinensis* (Table 3), while both attain the straight-hinge stage at approximately 40 hours, roughly twice the time described for *S. s. solidissima* by Ropes (1980). As pointed out by Costello et al. (1957) and Loosanoff & Davis (1963), culture temperatures play an important role in developmental times for marine bivalve larvae. *Spisula s. solidissima* attained ciliated blastula stage in < 24 hours when cultured at 21°C (Allen, 1953), but required 5 days to attain this stage when cultured at 25°C (Schechter, 1941). When cultured at 14°C, the straight-hinge stage for *S. s. solidissima* was attained in 72 hours, while at 22°C the stage was reached in 28 hours (Loosanoff & Davis, 1963). In a parallel study, *S. s. similis* larval development was faster at 25°C than at 20°C (Walker et al., in press).

Unfortunately, the pediveliger stage and size were not described for *S. sachalinensis* (Imai et al., 1983) or for *S. s. similis* in this study. For *S. s. similis,* 50% of animals were pediveligers at 107.3 μm in 7 days, whereas for *S. s. solidissima* a foot was observed in animals as small as 160 μm, with 80% of 215 μm and 100% of 240 μm animals possessing a foot (Loosanoff & Davis, 1963). *Spisula s. solidissima* metamorphoses at 280 μm in size and at 18 to 21 days (Costello et al., 1957). Loosanoff & Davis (1963) stated that *S. s. solidissima* metamorphoses at a size between 230 and 250 μm; while Chanley & Andrews (1971) reported that *S. s. solidissima* metamorphoses at 220–275 μm. Imai et al. (1983) stated 270 μm as the size that *S. sachalinensis* metamorphoses. In this study, *S. s. similis* had attained 50% pediveliger stage by day 7.5 with larvae at a mean size of 107.3 μm (Figure 2). Thus it appears that *S. s. similis* were close to setting before the cultures died at day 13 and that *S. s. similis* may metamorphose earlier and at a smaller size than *S. s. solidissima.* In previous and subsequent studies, *S. s. similis* was estimated to have metamorphosed between 18 to 19 days (Walker et al., 1995).

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